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Earthworms and the factors governing their distribution in an English beechwood

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With 19 figures

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1. Introduction

The study of earthworms (Lumbricidae) reported in this paper forms part of a research programme designed to investigate the ecosystem dynamics of a beech (*Fagus sylvatica* L.) woodland known as Brogden's Belt. Beech woods are typical of certain soil types in southern England (TANSLEY 1939) but according to SATCHELL (1967), who summarised many British earthworm studies, there appears to be no published account of Lumbricidae from beechwoods in Britain.

The present research rectifies this situation; it provides data on site characteristics and an assessment of species composition, diversity and equitability. Species associations are described and analyses of the factors affecting the distribution of the ten earthworm species found on the site are given.

2. Site description and summary of site characteristics

Brodgen's Belt (Nat. grid ref. SU 464077) is a narrow belt of beech, approximately 450 × 75 m and has a longitudinal axis aligned in a NNW-SSE orientation. It lies towards the centre of Wytham Estate at an altitude of 150 m and is located on the perimeter of Wytham Great Wood, a mixed woodland of oak (*Quercus robur* L.), ash (*Fraxinus excelsior* L.), sycamore (*Acer pseudoplatanus* L.). hornbeam (*Carpinus betulus* L.), sweet chestnut (*Castaneus sativa* MILL.) and birch (*Betula pendula* ROTH.) as well as beech. Brodgen's Belt, like many other existing beechwoods in the south of England, is a product of nineteenth century afforestation of sheep walk. Is was planted between 1814 and 1827 (GRAYSON and JONES 1955) and is situated on araised tropical fringing reef of Jurassic limestone ("Coral rag") of the Upper Corralian strata (ARKELL 1945; ELTON 1966). To the east lies Lower Seeds, an area of arable farmland; Upper Seeds, which lies to the west,is also under cultivation although the southerntip of Brodgen's, where the studie side wgs located, is bounded on its western side by an area of ungrazed *Brachypodium pinnatum* (L.) BEAUVOIS grassland known as the Dell. Brodgen's was declared a biological reserve some twenty years ago but even before then was notsubject to intensive management; it had thus been allowed to mature with a minimum of interference.

The study site, located at the southern end of Brodgen's Belt, was established as a series of 10 × 10 m grid squares (fig. 1a) and covered an area of 5130 m². The rendzina type soil is shallow (6—42 cm in depth), overlies broken "Coral Rag", and, with a single exception (*p*H 6.3), has a range of *p*H's from 7.3 to 8.0 (fig. 1a). Of the forty trees, excluding seedlings, located within the experimental grid twenty nine were beech. The remaining eleven comprised three sycamore (*A. pseudoplatanus* L.), two lime (*Tilia europaea* L.), two elm (*Ulmus procera* SALISBURY), three oak (*Q. robur* L.) and one larch (*Larix decidua* MILL.). Fig. 1b shows those areas of the grid where the soil depth is greater than, or less than, 25 cm. Fig. 1c and 1d show the canopy cover and ground flora cover respectively in May-June 1973. The ground flora is sparse and its general distribution reflects those gaps in the canopy which persist longest during early Spring.

Between late May 1969 and May 1973 the ground flora was mapped, and sampled on thirteen occasions to determine peak standing crops. Table 1 shows the species present and indicates by means of an asterisk those considered important. Importance in this context was defined as those species whose individual peak standing crop biomass exceeded ten per cent of the sum of the peak standing

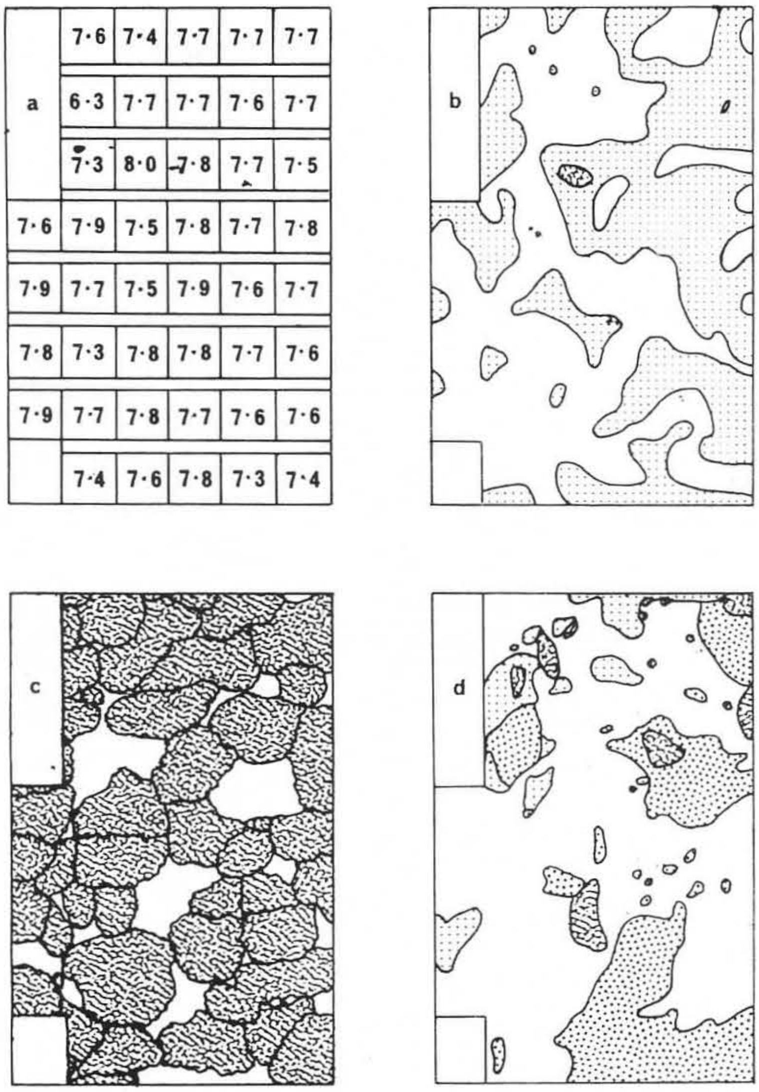


Fig. 1. Maps of major site characteristics; (a) the 10 × 10 m grid squares and their soil pH values (b) soil depth: unshaded areas — < 25 cm, dotted areas — > 25 cm, the stippled area represents a badger sett (c) full canopy cover: unshaded areas — gaps in canopy (d) ground flora cover: unshaded areas — bare litter, irregular dots — *Mercurialis perennis*, regular dots — Gramineae, stippling — *Rubus fruticosus* agg.

crops of the category to which they belonged (woody or non-woody) in at least two out of the three years 1969—1970, 1970—1971 and 1971—1972. Of the thirty nine species recorded four woody plants (*Rubus fruticosus* L. agg.; seedlings of *A. pseudoplatanus* L., *Crataegus monogyna* JACQUIN and *F. sylvatica* L.), one grass [*B. sylvaticum* (L.) BEAUVOIS] and one herb (*Mercurialis perennis* L.) were designated important.

The standing crop of litter derived from the ground flora and trees on the site was sampled, via 80 stratified random sited sample units (181.5 cm²) per sampling occasion, at two monthly intervals from February 1971 to January 1973. Brogden's Belt is subject to south-westerly prevailing winds and the leaf litter of which beech leaves constituted 62.56, 23.21, 60.87 and 53.23 % respectively in each of the years 1969—1970, 1970—1971, 1971—1972 and 1972—1973 does not remain where it falls and is redistributed by wind action. Litter data relevant to the present study concern only

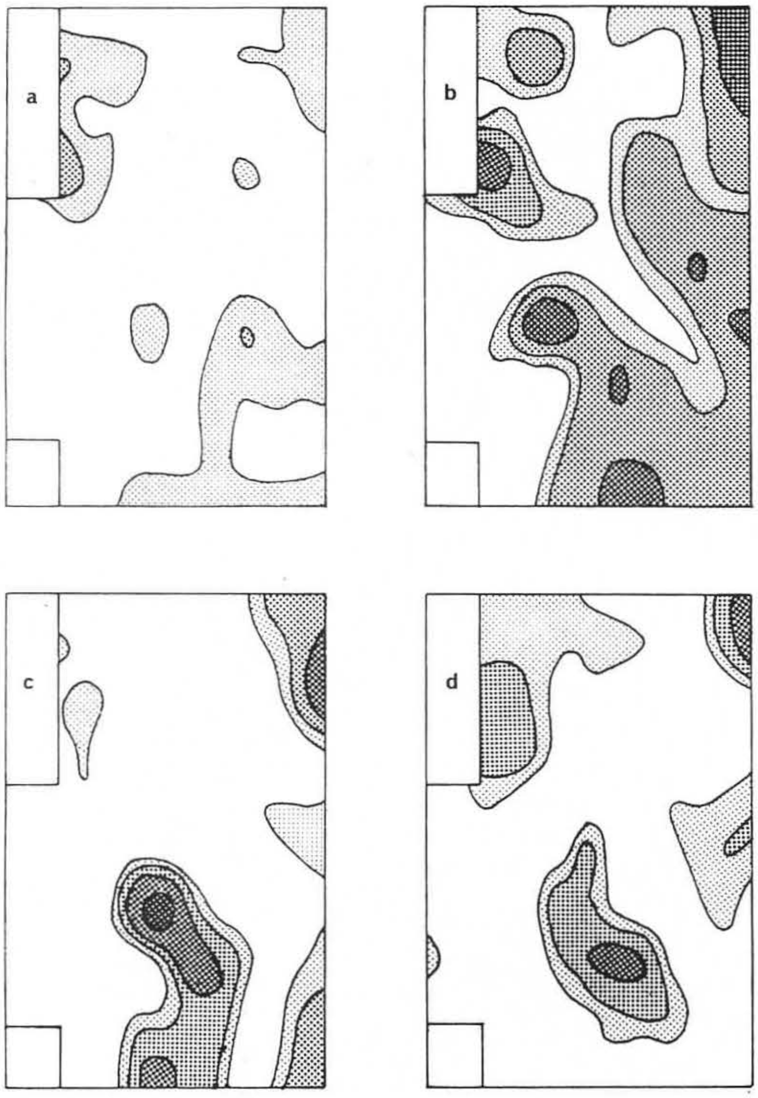


Fig. 2. Computer derived maps of leaf litter standing crop; (a) September, 1971 (b) January, 1972 (c) May, 1972 (d) September, 1972. Areas from unshaded to dark shaded represent 0—250, 250—500 500—1000, 1000—2000 and > 2000 g m^{-2} respectively.

those components which move easily in the wind and are most readily available to earthworms; namely leaves, flowers and budscales as opposed to twigs, bark and tree fruits. Fig. 2 a—d show distribution maps derived from computer drawn contours of leaf litter standing crop in September 1971, January, May and September 1972. Note that the greatest amounts of litter accumulated in those areas shown in fig. 1 d to be covered by ground vegetation. It is clear that the vegetation traps much of the leaf litter as it is blown about the woodland floor.

Soil depth was determined by means of a metal rod of 1 cm diameter which was hammered into the soil at 420 regularly spaced points on the grid. The computer determined 25 cm depth contour map obtained via results from the latter method is shown in fig. 1 b. Comparison of this figure with fig. 2 b leaves little doubt that differential accumulation of leaf litter over the years is reflected in the different soil depths recorded over the study site.

Table 1. The flowering plants recorded in the ground/field zone of Brodgen's Belt between October 1969 and October 1972

Woody plants
* *Acer pseudoplatanus* L.
* *Rubus fruticosus* L. agg.
Rosa canina L.
* *Crataegus monogyna* Jacquin
Ulmus procera Salisbury
* *Fagus sylvatica* L.
Quercus robur L.

Non-woody plants
Ranunculus bulbosus L.
Viola riviniana Reichenbach
Stellaria media (L.) Villars
Moehringia trinervia (L.) Clairville
Potentilla sterilis (L.) Garcke
Fragaria vesca L.
Geum urbanum L.
Rosa canina L.
Epilobium montanum L.
Circaea lutetiana L.
Sanicula europaea L.

Non-woody plants (continued)
* *Mercurialis perennis* L.
Urtica dioica L.
Primula veris L.
Galeobdolon luteum Huds.
Glechoma hederacea L.
Galium verum L.
Senecio vulgaris L.
Taraxacum officinale Weber
Endymion non-scriptus (L.) Garcke
Cephalanthera damasonium (Miller) Druce
Carex sylvatica Hudson
Festuca gigantea (L.) Villars
Festuca rubra L.
Lolium perenne L.
Poa nemoralis L.
Poa pratensis L.
Dactylis glomerata L.
* *Brachypodium sylvaticum* (Hudson) Beauvois
Brachypodium pinnatum (L.) Beauvois
Deschampsia cespitosa (L.) Beauvois
Agrostis stolonifera L.

Note. — Species whose individual peak standing crop biomass exceeded ten per cent of the sum of the peak standing crops of the category to which they belonged (woody or non-woody) in at least two out of the three years of study are marked with an asteriks.

Litter standing crop and soil depth could have a marked effect on earthworm distribution but other possible influential factors considered were pH, soil density, soil water content and changes in soil water content (drying out).

For the measurement of pH, 10 g of soil were taken from the centre of each grid square, and 25 ml of 1 M KCl added. After one hour had elapsed the pH determinations were made with a Philips portable pH meter. Fig. 1 a shows the results obtained.

Soil density (dry wt. soil/vol. soil core expressed as g ml^{-1}) was determined from soil cores taken near the centre of each grid square on each of eleven separate occasions between June and Auguste. Fig. 3 a shows a computer derived map drawn from the mean density values of each grid square.

The soil density samples were also used in the calculation of soil water content (wt. of water/vol. soil core expressed as g ml^{-1}). Fig. 3 b shows a map of the maximum soil water contents measured during June to August.

On 27 June 25.1 mm of rain fell and on 16 July a further 12.8 mm; soil samples were taken on both these dates and in conjunction with results from later samples it proved possible to calculate The percentage decrease in water content over two separate periods, June—July and July—August. the obtained figure were used as an indication of the drying out properties of the soil in summer and Fig. 3 a and 3 d show maps of this characteristic.

3. Earthworm sampling

From October 1971 to September 1972 earthworms were sampled at intervals of one month and between November 1972 and October 1973 every three months. Data from both years were used in calculating species dominance indices (table 2) but only the first year data were employed in the analysis of factors thought to influence earthworm distribution.

On each sampling occasion twenty two sample units, selected on a stratified random basis, were taken. The relevant material from each sample unit comprised worms sorted by hand from a soil core (obtained by means of a square metal corer, 25 cm on the side, which was forced rapidly into the substrate with blows from a sledge hammer) and worms extracted from the 25 × 25 cm sample hole by the application of 4% formalin. The formalin solution was applied via a watering can with sprinkler at 10 min intervals over a period of 30 min, nine litres of solution were used for each extraction.

In addition to the 264 sample units obtained in the above way during the first year 32 circular sample units (0.0189 m^2) of litter were taken in a stratified random manner each month. These were processed in a K.L.G. infra-red extractor (Kempson et al. 1963) over a period of ten days.

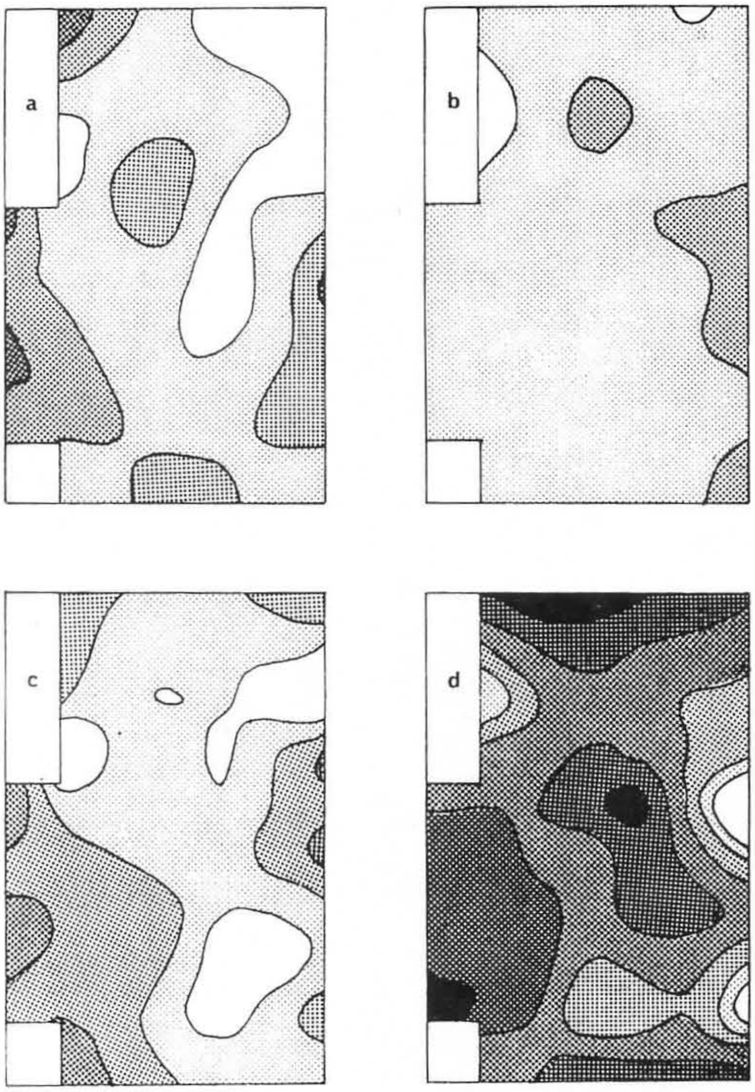


Fig. 3. Computer derived maps of selected soil characteristics; (a) soil density: areas from unshaded to dark shaded represent 0.5—0.6, 0.6—0,7, 0.7—0.8, 0.8—0.9 and >0.9 g ml^{-1} respectively (b) maximum soil water content during June—August: areas from unshaded to dark shaded represent 0.3—0.4, 0.4—0.5 and 0.5—0.6 g ml^{-1} respectively (c) drying out properties in June and July: areas from unshaded to darks shaded represent decreases in water content of 0—10, 10—20, and 20—30 per cent g^{-1} of soil (d) drying out properties in July and August: areas from unshaded to dark shaded represent decreases in water content of 0—10, 10—20, 20—30, 30—40 and 40—50 per cent g^{-1} of soil respectively.

Table 2. The annual mean density, proportional abundance (*Pi*) and numerical rank of the ten earthworm species collected between October 1971 and September 1973

	Oct. 1971—Sept. 1972			Oct. 1972—Sept. 1973		
	No. m^{-2}	*Pi*	Rank	No. m^{-2}	*Pi*	Rank
Allolobophora caliginosa (SAVIGNY 1826)	53.4	0.386	1	46.9	0.399	1
Allolobophora rosea (SAVIGNI),1826	34.4	0.249	2	30.9	0.263	2
Allolobophora muldali (GATES 1958)	12.4	0.090	3	4.4	0.037	6
Lumbricus terrestris (LINNAEUS 1758)	9.1	0.066	4	14.4	0.122	3
Octolasion cyaneum (SAVIGNY 1826)	7.5	0.054	5 =	4.0	0.034	7
Dendrobaena mammalis (SAVIGNY 1826)	7.5	0.054	5 =	6.2	0.053	4
Lumbricus castaneus (SAVIGNY, 1826)	6.7	0.048	7	5.8	0.049	5
Allolobophora longa UDE 1885	3.6	0.026	8	3.1	0.026	8
Allolobophora chlorotica (SAVIGNY 1826)	3.0	0.022	9	1.3	0.011	9
Dendrobaena rubida (SAVIGNY 1826)	0.6	0.004	10	0.6	0.005	10
Total	**138.2**	**0.999**		**117.6**	**0.999**	

4. Earthworm species composition, diversity and equitability

Of the 27 species of the family Lumbricidae recorded from the British Isles (GERARD 1964) ten were found in the study area. The species collected are listed in Table 2, where they are ranked according to their proportional abundance *(Pi)* in each of the two years of sampling. The abundance rankings of the two most common and the three least common species remained the same in each of the years 1971—1972 and 1972—1973, whereas those of the remaining five species differed between the two years. Note that during 1971—1972 and 1972—1973 *Allolobophora caliginosa* and *Allolobophora rosea* together dominated the earthworm community with combined dominance indices of 0.635 in the first year and 0.652 in the second. Clearly, one fifth of the total number of earthworm species contributed more than three fifths of the total number of individuals present in the study area.

Indices of species diversity and equitability of abundance provide some indication of the ecological "fullness", or the maximum ecological diversity attainable, of a community (SOUTHWOOD 1966) and were used as such in the prevent study. The indices calculated were Simpson's index, the Shannon-Wiener function and Lloyd and Ghelardi's equitability indices; all are detailed in SOUTHWOOD (1966). Table 3 shows the indices applicable to the study area and to two Swedish beechwoods described by NORDSTRÖM and RUNDGREN (1973).

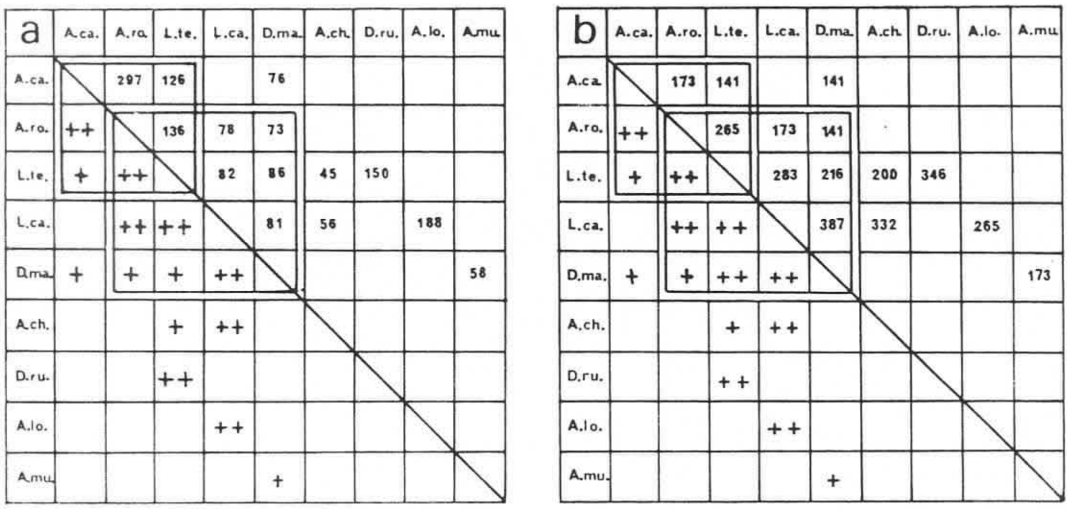
Table 3. Indices of species diversity and equitability of abundance for three beech woodlands

Locality	No. of spp.	Simpson's Index $1 \sum_{i=1}^{s} (Pi)^2$	Shannon-Wiener function (H)	Equitability Index (H/H_{max})	Lloyd & Ghelardi index (s'/s)
Brodgen's Belt, U.K.					
1971—1972	10	0.77	2.56	0.77	0.80
1972—1973	10	0.75	2.44	0.73	0.70
Beech Wood 4 (Sweden)	6	0.75	2.14	0.83	1.00
Beech Wood 17 (Sweden)	8	0.83	2.70	0.90	1.00

The Simpson indices and Shannon-Wiener functions indicate relatively high species diversity in all three woods. However, the Lloyd and Ghelardi index $\left(\frac{s'}{s}\right)$ suggests that the ten species found in Brodgen's Belt constitute only 70—80 per cent of the total number of earthworm species that might be accommodated in this habitat. In contrast the two Swedish woodlands, with 6 and 8 species might be considered ecologically full with respect to earthworms.

5. Earthworm species associations and ordination

Species diversity and equitability indices do not provide any indication of the degree of association or similarity of the species present in a habitat. For this purpose indices of similarity or recurrence have been proposed; amongst these are Sorensen's Quotient of Similarity, Cole's Coefficient of Similarity, Fager's Recurrent Grouping and Montford's Ordination, all of which are described in SOUTHWOOD (1966).



a	A.ca.	A.ro.	L.te.	L.ca.	D.ma.	A.ch.	D.ru.	A.lo.	A.mu.
A.ca.		297	126		76				
A.ro.	++		136	78	73				
L.te.	+	++		82	86	45	150		
L.ca.		++	++		81	56		188	
D.ma.	+	+	+	++					58
A.ch.			+	++					
D.ru.			++						
A.lo.				++					
A.mu.					+				

b	A.ca.	A.ro.	L.te.	L.ca.	D.ma.	A.ch.	D.ru.	A.lo.	A.mu.
A.ca.		173	141		141				
A.ro.	++		265	173	141				
L.te.	+	++		283	216	200	346		
L.ca.		++	++		387	332		265	
D.ma.	+	+	++	++					173
A.ch.			+	++					
D.ru.			++						
A.lo.				++					
A.mu.					+				

Fig. 4. Species associations illustrated in the form of trellis diagrams; (a) according to SØRENSEN's quotient (b) according to COLE's index. Two crosses represent the 10 % level of significance and one cross indicates the 5 % level.

Fig. 4a and b respectively show Sorensen's Q/S and Cole's C_{AB} values arranged in the form of trellis diagrams where the indices giving the highest similarity values are arranged nearest to the diagonal. Using the index values which showed a statistically significant association both methods of analysis distinguished the same two species associations.

Association A.: *A. rosea, L. terrestris, L. castaneus, D. mammalis.*

Association B.: *A. rosea, A. caliginosa, L. terrestris.*

Analysis by Fager's recurrent grouping also gave rise to two species associations, both of equivalent rank.

Association A.: *L. terrestris, D. mammalis, A. rosea, L. castaneus.*

Association B.: *L. terrestris, D. mammalis, A. rosea, A. caliginosa.*

In the event of two associations of equivalent rank appearing, FAGER (1957) recommends that the association which occurs as a unit in the greatest number of samples be selected. On this criterion Association A, as distinguished by all three methods of analysis, becomes the "association" and all the other species bar *O. cyaneum* become associates. Fig. 5 was constructed using Cole's C_{AB} indices and the significance of association determined from the χ^2 values of the 2×2 contingency tables used to calculate C_{AB}; it supports the choice of Association A according to Fager's criterion. Clearly, *L. terrestris, D. mammalis, A. rosea*

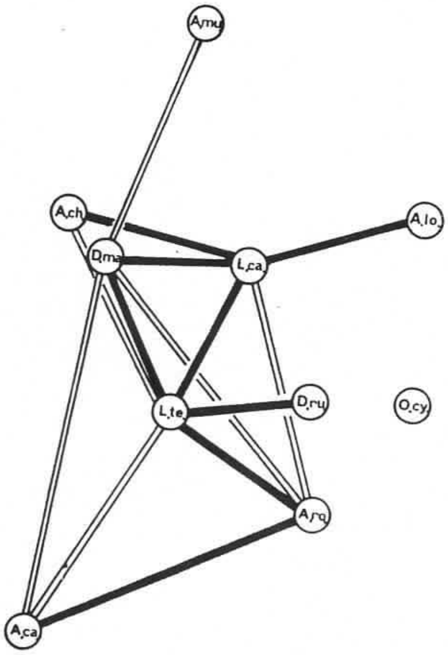


Fig. 5. Diagram illustrating the three dimensional nature of species groupings according to the Cole *AB* index. Species shown are *A. caliginosa (A. ca.)*, *A. chlorotica (A. ch.)*., *A. longa (A. lo.)*, *A. muldali (A. mu.)*, *A. Rosea '(A. ro.)*, *D. mammalis (D. ma.)*, *D. rubida (D. ru.)*, *L. castaneus (L. ca.)*, *L. terrestris (L. te.)*, and *O. cyaneum (O. cy.)*. Significant associations at $p < 0.01$ and $p < 0.05$ are indicated by solid and double lines respectively.

and *L. castaneus* are all positively associated with one another at a high level of significance. *A. caliginosa*, which replaces *L. castaneus* in Association B, shows positive associations at a lower level of significance with *L. terrestris*, *D. mammalis* and *A. rosea* than does *L. castaneus*.

The fact that species occur as an association does not mean that their requirements are necessarily similar, only that they occur together regularly. Ordination is a method of analysis from which similarity in requirements can be inferred and fig. 6 was constructed following the method of MOUNTFORD (1962). Note the implied close similarities of requirements between *D. ruida* and *L. terrestris*, *D. mammalis* and *L. castaneus*, and *A. rosea* and *A. caliginosa*. b

6. Earthworm distribution

6.1. Total earthworms

Fig. 7a—d show "relief" maps derived from computer drawn contours of the distribution and numbers of the total earthworm fauna of Brodgen's Belt. Comparison of these maps with those for soil depth, ground flora, leaf litter standing crop, soil density, soil water content and drying out properties (fig. 1—3) gives no clear indication as to which, if any, of these parameters are correlated with the distribution of the total earthworm fauna but suggests that soil depth, ground flora and possibly litter standing crop might be implicated. The fact that no clear picture emerges regarding the factors affecting total earthworm distribution is not surprising when one considers the different life styles of the ten species comprising the lumbricid fauna of Brodgen's Belt.

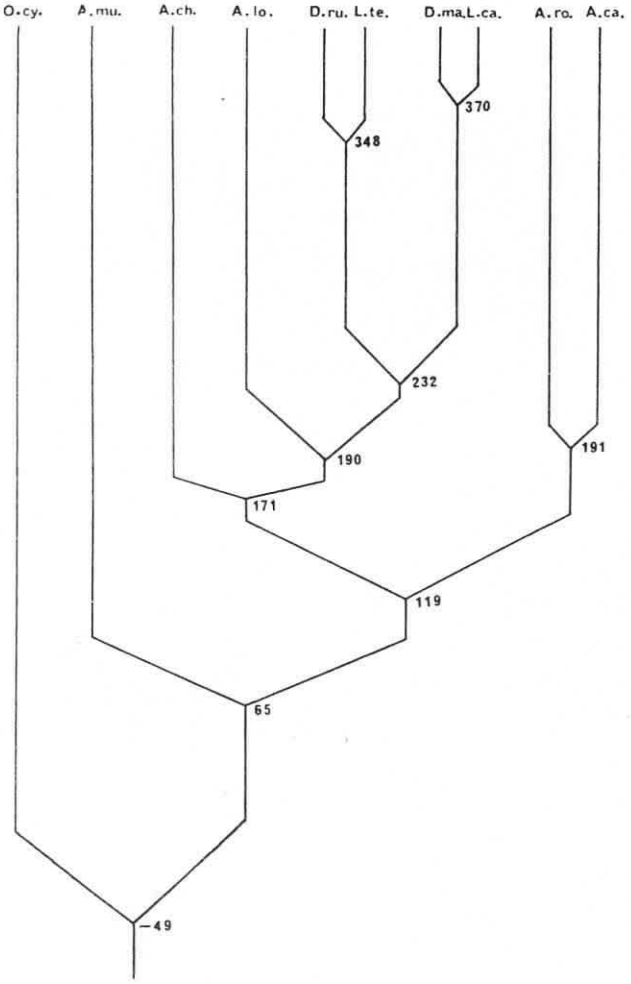


Fig. 6. Dendogram of species similarities according to Mountford's index. Species abbreviations as in figure 5.

According to Bouché (1972) nine of the ten species found on the site can be assigned to one of three life style categories, these are: Epigées (*D. mammalis*, *L. castaneus* and *D. rubida* are of this type and are primarily litter dwellers), Anécique (*L. terrestris* and *A. longa* belong to this category; they construct deep vertical burrows, produce surface casts and come to the surface at night to draw down litter) and Endogées (*A. caliginosa*, *A. rosea*, *A. muldali* and *O. cyaneum* can be assigned to this group in that they construct branching, horizontal burrows and live constantly in the mineral-organic substrate). *A. chlorotica*, the remaining species, is considered intermediate in character.

Clearly, the different life styles of each of the species could affect the overall picture of total earthworm distribution and it was decided to examine separately the distribution of individual species via computer derived maps.

6.2. Litter dwellers (Epigées)

Fig. 8a—d show the distribution and numbers of *D. mammalis* as ascertained by (i) hand sorting and formalin extraction and (ii) litter extraction by the method of Kempson et al. (1963). Maps were drawn for each of the four three month periods between October

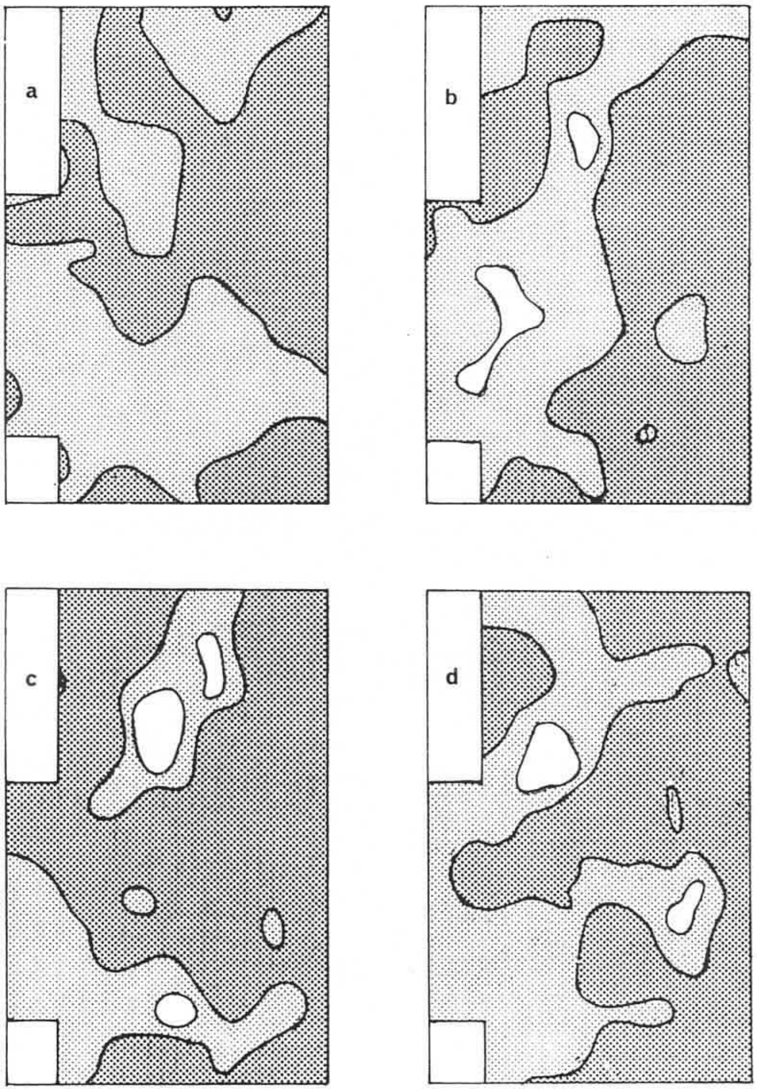


Fig. 7. Computer derived distribution maps of the total earthworm fauna; (a) October—December, 1971 (b) January—March, 1972 (c) April—June, 1972 (d) July—September, 1972. Areas from unshaded to dark shaded represent 0—10, 10—100 and > 100 m^{-2} respectively.

1971 and September 1972 but those used in illustration relate to January—March 1972 when the leaf litter was moist and July—September 1972 when it was subject to drying out. The primarily litter dwelling habit of *D. mammalis* is very obvious during January—March (fig. 8a compared with 8b) and the distribution shows good agreement with that of the litter standing crop in January 1972 (fig. 2b). However, during the July—September period this species apparently inhabits soil in preference to litter (fig. 8c compared with 8d); this view is reinforced by the lack of coincidence of *D. mammalis* distribution and that of the litter standing crop in either May or September 1972 (fig. 8c compared with 2c and 2d). From the data presented it can be inferred that *D. mammalis* is affected by the drying out of the litter and either dies in situ or moves into the soil during dry periods. Fig. 9 shows that both processes are involved, numbers in the litter are high during the winter months

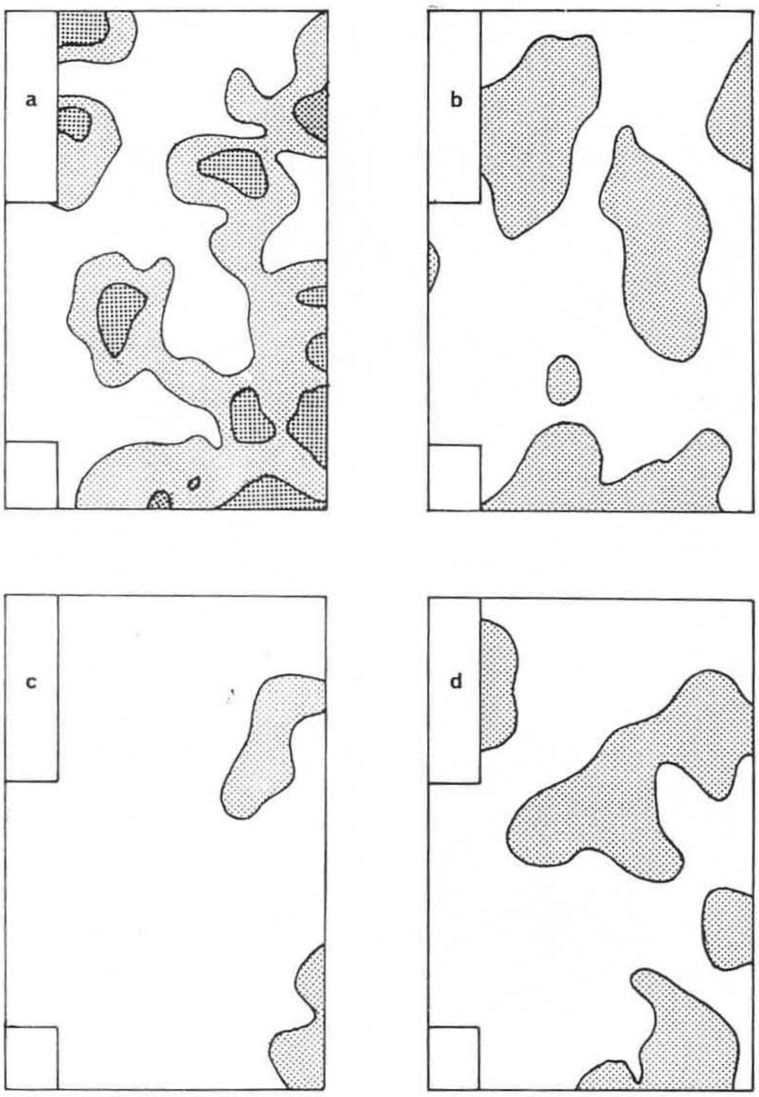


Fig. 8. Computer derived distribution maps of D. mammalis; (a) infra-red extraction from litter — January to March, 1972 (b) hand sorted and formalin extracted — January to March 1972 (c) infra-red extraction from litter — July to September, 1972 (d) hand sorted and formalin extracted — July to September, 1972. Areas from unshaded to dark shaded represent 0—10, 10—100 and > 100 m^{-2} respectively.

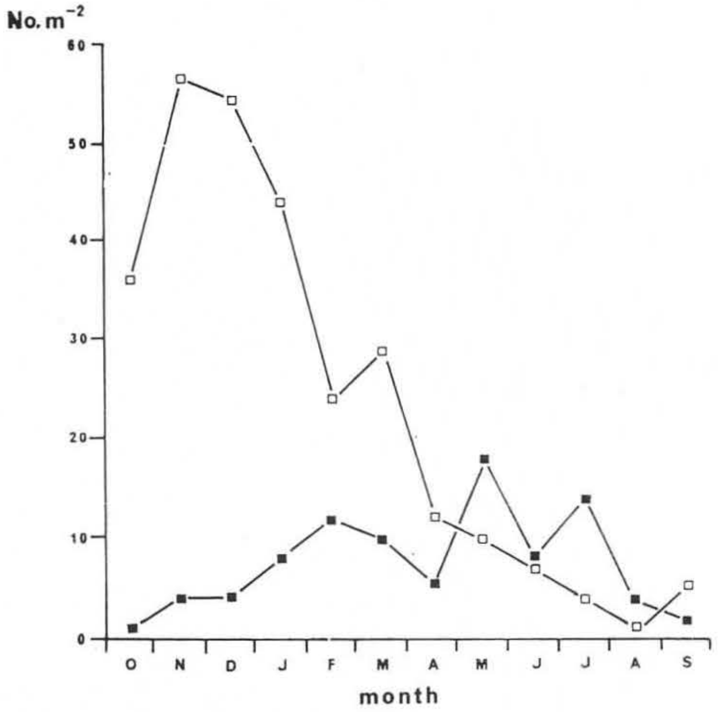


Fig. 9. *D. mammalis*: seasonal numbers m^{-2} estimated by infra-red extraction of litter (open squares) and hand sorting and formalin extraction (closed squares).

but decrease through spring into late summer and autumn, the converse occurs in the soil but there is a decrease in overall numbers through spring, summer and autumn.

Fig. 10a—d show the distribution and numbers of *L. castaneus* in the litter and in the soil over the same time periods as were used for *D. mammalis*. The relationship of distribution and numbers of the litter inhabiting *L. castaneus* to litter standing crop at all seasons is clear (Fig. 10a and 10c compared with 2b—d). However, as shown by fig. 10b, considerable numbers occur in the soil during January to March. Fig. 11 shows that during winter and spring *L. castaneus* numbers were approximately equal in both litter and soil but that in both instances mortality occurred such that numbers were much reduced by March. Through the summer and autumn numbers continued to decline in the soil (see also fig. 10d) but increased once more in the litter. The increase can be accounted for by either reproduction or immigration, the former being the most probable. Unlike *D. mammalis*, *L. castaneus* does not appear to be adversely affected by the drying out of litter in spring and early summer; nevertheless there is an overall reduction in numbers through late summer and autumn.

D. rubida, the third of the litter dwellers, occurred at too low a density on the site ($0.6\ m^{-2}$) to permit analysis of the type described for *D. mammalis* and *L. castaneus*. Fig. 12 shows its limited distribution during the period October 1971 to September 1972.

6.3. Deep burrowers (Anécique)

Fig. 13a—d show the distribution and numbers of L. *terrestris* as determined by hand sorting and formalin extraction. On an annual basis this species is widespread and more numerous over the site than any of the three species considered so far. Comparison of fig. 13a—d with the maps of the various site characteristics shown in fig. 1—3 indicates

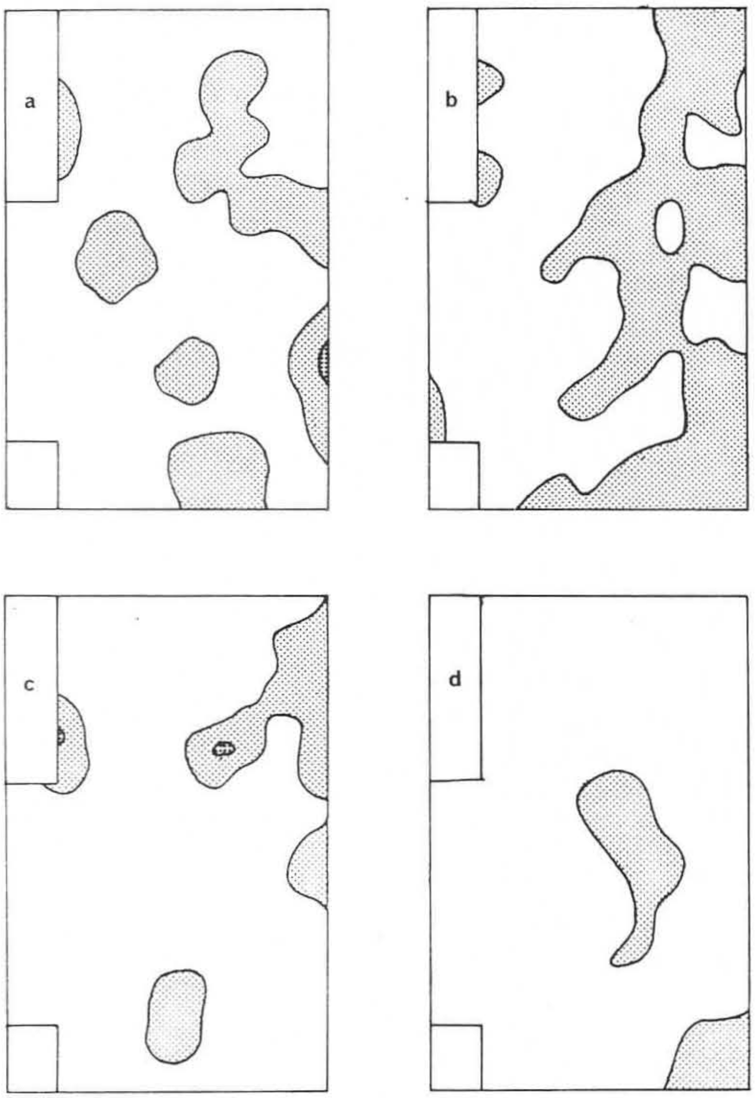


Fig. 10. Computer derived distribution maps of *L. castaneus*; (a) infra-red extraction from litter — January to March, 1972 (b) hand sorted and formalin extracted — January to March, 1972 (c) infra-red extraction from litter — July to September, 1972 (d) hand sorted and formalin extracted — July to September, 1972. Areas from unshaded to dark shaded represent 0—10, 10—100 and > 100 m^{-2} respectively.

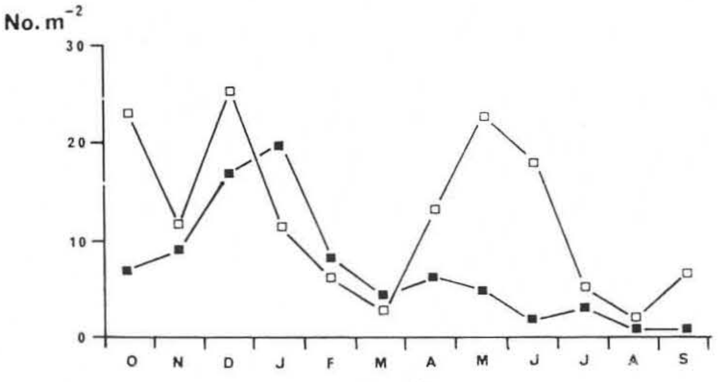


Fig. 11. *L. castaneus*: seasonal numbers m^{-2} estimated by infra-red extraction of litter (open squares) and hand sorting and formalin extraction (closed squares).

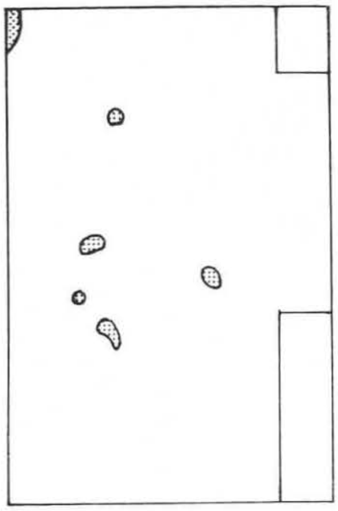


Fig. 12. Computer derived distribution map of *D. rubida*. Based on monthly collections between October, 1971 and September, 1972. Areas from unshaded to dark shaded represent 0—10 and > 10 m^{-2} respectively.

that the distribution pattern of *L. terrestris* is most likely to be associated with soil depth fig. 1 b) or ground flora cover (fig. 1 d).

A. longa, the remaining deep burrower, occurred at too low a density on the site (3.6 m^{-2}) to permit computer mapping and analysis on a quarterly basis. Fig. 14 shows the numbers and distribution of this species as determined from a full year's data. Comparison of the distribution map (fig. 14) with the maps of the site characteristics (fig. 1—3) indicates possible associations with soil depth (fig. 1 b) and ground flora cover (fig. 1 d). In this respect *A. longa* appears superficially not unlike *L. terrestris*.

6.4. Horizontal burrowers (Endogées)

The majority of the lumbricid species found in Brogden's Belt are referable to this category.

Fig. 15 a and b show that *A. caliginosa*, the most numerous species (53.4 m^{-2}) was widespread over the site. Comparison of these two figures with maps of site characteristics

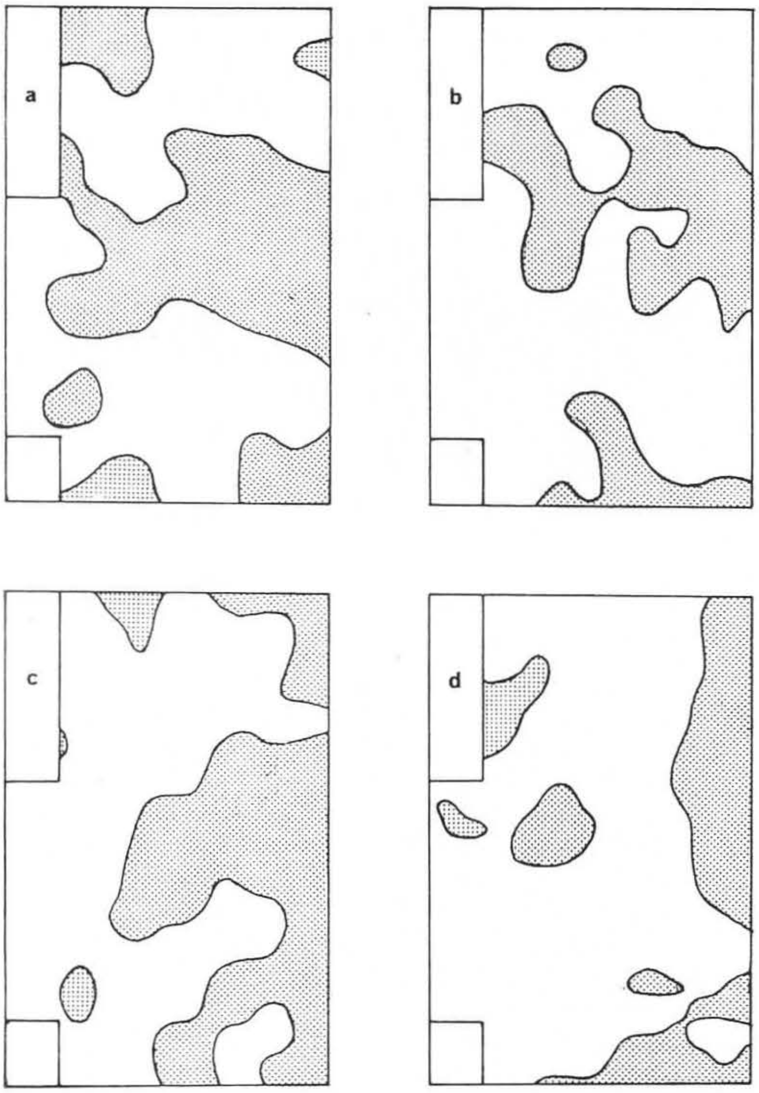


Fig. 13. Computer derived distribution maps of *L. terrestris*; (a) October—December, 1971 (b) January—March, 1972 (c) April—June, 1972 (d) July—September, 1972. Areas from unshaded to dark shaded represent 0—10 and > 10 m^{-2} respectively.

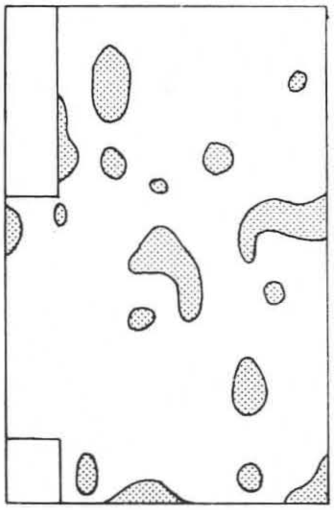


Fig. 14. Computer derived distribution map of *A. longa*. Based on monthly collections between October, 1971 and September, 1972. Areas from unshaded to dark shaded represent 0—10 and > 10 m^{-2} respectively.

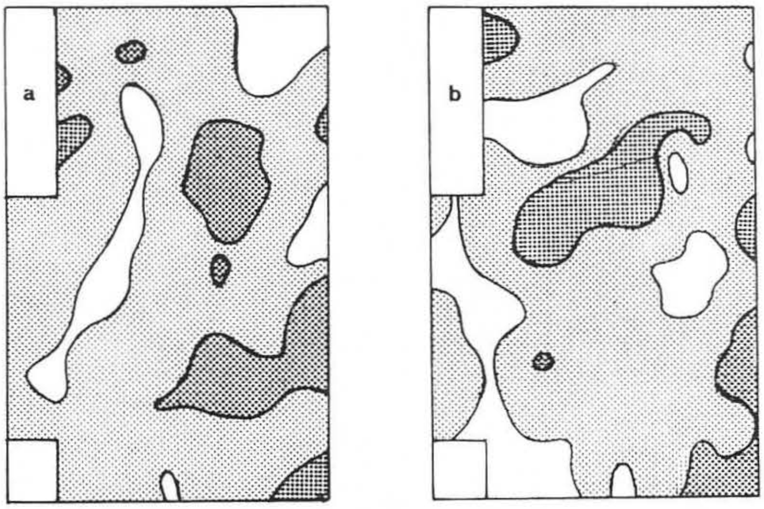


Fig. 15. Computer derived distribution maps of *A. caliginosa*; (a) January—March, 1972 (b) July to September, 1972. Areas from unshaded to dark shaded represent 0—10, 10—100 and > 100 m^{-2} respectively.

fig. 1—3) give no clear indication of those factors which might be correlated with population density or distribution.

A. rosea, the second most numerous earthworm (34.4 m^{-2}) was also widely distributed over the site (fig. 16a and b) but in this case there appears to be a relationship between the *A. rosea* density and soil depth (fig. 1b).

A. muldali, a little known British species, was found in quite large numbers (12.4 m^{-2}) and fig. 17a—d show that it occurred all over Brodgen's Belt. Comparison of its distribution maps with those of the site characteristics (fig. 1—3) indicate a possible association with leaf litter standing crop (fig. 2a—d).

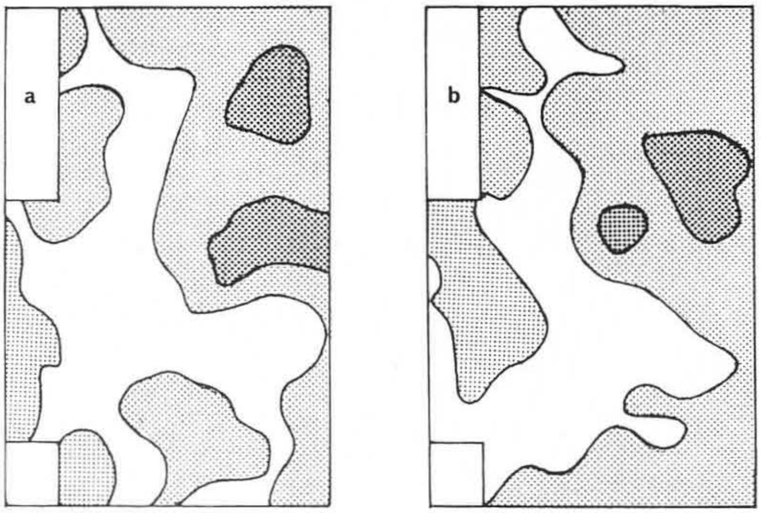


Fig. 16. Computer derived distribution maps of *A. rosea*; (a) January—March, 1972 (b) July—September, 1972. Areas from unshaded to dark shaded represent 0—10, 10—100 and > 100 m^{-2} respectively.

O. cyaneum was relatively common on the site (7.6 m^{-2}) and fig. 18a—d show density distribution maps for each of the four quarters of the period October 1971 to September 1972. Comparison of these distribution maps with those of the various site characteristics fig. 1—3) gives no indication of any factors that might be correlated with population density or distribution.

6.5. Intermediate category

A. chlorotica, which occurred in very low numbers (3.0 m^{-2}) is the only member of this group. Fig. 19 shows the density distribution of this species over the full twelve months of study. It can be seen that the highest densities occurred on the eastern side of Brogden's Belt. Comparison of the distribution of *A. chlorotica* (fig. 19) with the distribution maps of site characteristics (fig. 1—3) failed to reveal any obvious correlations.

7. Factors governing earthworm distribution

The uneven distribution of earthworms within Brogden's Belt has been demonstrated by means of the distribution maps derived from computer drawn contour plots. However, visual comparison of the maps (fig. 7—8, 10, and 12—19) with those of site characteristics (fig. 1—3), although giving some indication, is not sufficient to determine convincingly those factors affecting earthworm distributions. To achieve this purpose data extracted from the original contour plots of site characteristics and earthworm density distribution were subjected to linear multiple regression analysis. Data suitable for the analysis were obtained by placing a transparent outline of the grid (fig. 1a) over each site characteristic and earthworm density contour map; data points were considered to lie at the centre of each 10 × 10 m grid square and hence 44 units of information were read from each contour map. For each of the ten earthworm species the site characteristics examined were soil *p*H, soil depth, soil density, leaf litter standing crop, maximum soil water content during June ot August, soil drying out properties during June—July and July—August.

The results of the regression analysis are summarised in table 4. It can be seen from the table that approximately 40% of the total earthworm distribution can be explained in terms of soil depth, density, water content and litter standing crop. The litter dwellers

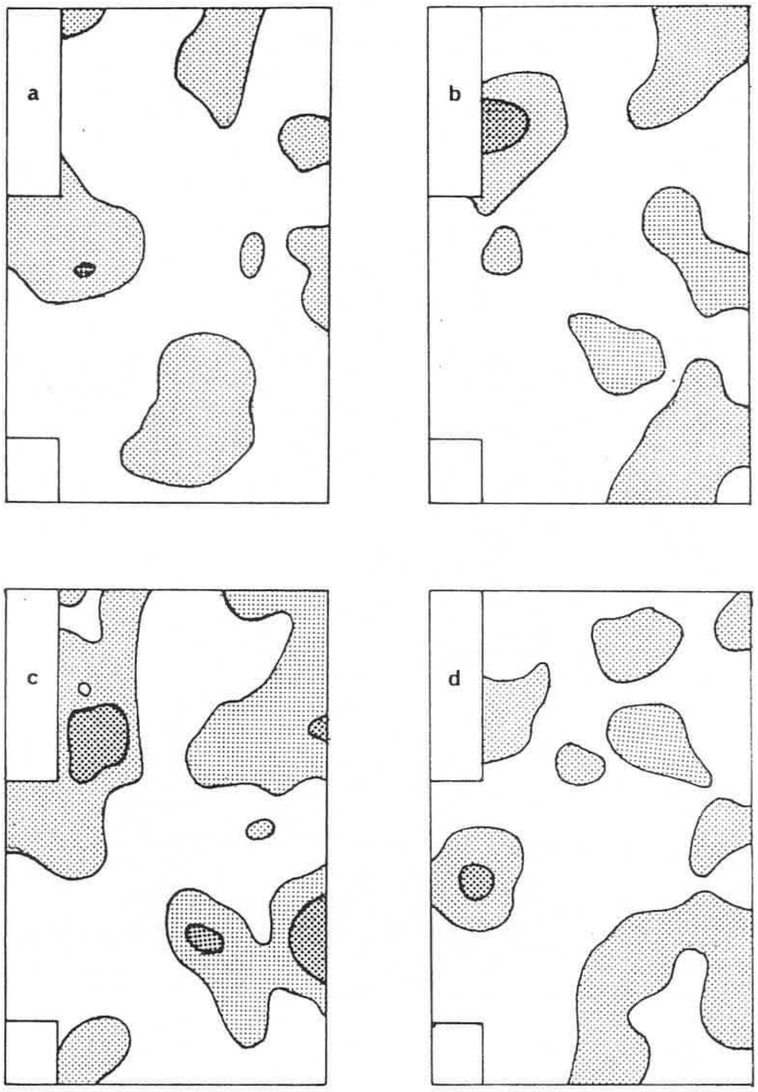


Fig. 17. Computer derived distribution maps of *A. muldali*; (a) October—December, 1971 (b) January—March, 1972 (c) April—June, 1972 (d) July—September, 1972. Areas from unshaded to dark shaded represent 0—10, 10—100 and > 100 m^{-2} respectively.

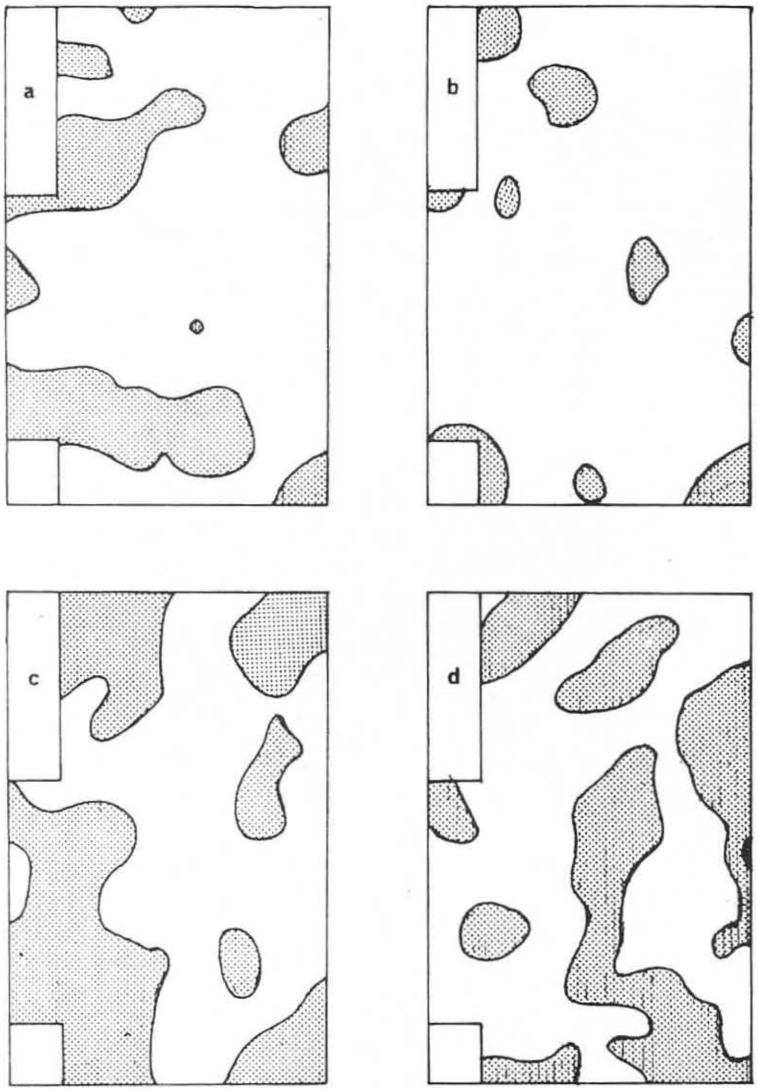


Fig. 18. Computer derived distribution maps of *O. cyaneum* (a) October—December, 1971 (b) January—March, 1972 (c) April—June, 1972 (d) July—September, 1972. Areas from unshaded to dark shaded represent 0—10, 10—100 and > 100 m^{-2} respectively.

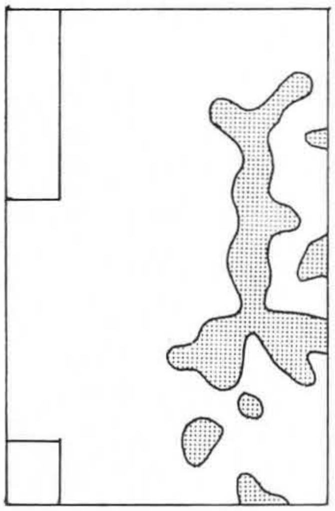


Fig. 19. Computer derived distribution map of *A. chlorotica*. Based on monthly collections between October, 1971 and September, 1972. Areas from unshaded to dark shaded represent 0—10 and $> 10\ m^{-2}$ respectively.

Table 4. The results obtained by multiple regression analysis of earthworm numbers and various site characteristics

Earthworm species	Factors in order of significance of correlation with earthworm distribution	F with 43 d.f.	P	Percentage of variance explained by the factors identified in column 2
Total earthworms	1. soil depth 2. soil density 3. max. water content (Jn.-Aug.) 4. litter standing crop	11.818	0.01	42.4
Epigées:				
D. mammalis (litter)	1. soil depth 2. drying out (Jn.—Jly.) 3. litter standing crop	7.434	0.01	28.7
D. mammalis (soil)	none	—	—	—
L. castaneus (litter)	1. max. water content (Jn.—Aug.) 2. drying out (Jn.—Jly) 3. litter standing crop	9.097	0.01	32.1
L. castaneus (soil)	1. soil depth 2. soil density	8.282	0.01	26.9
D. rubida	1. drying out (Jn.—Jly.)	4.948	0.05	10.5
Anécique:				
L. terrestris	1. soil depth	11.734	0.01	21.8
A. longa	1. drying out (Jly.—Aug.)	5.756	0.05	12.1
Endogées:				
A. caliginosa	1. litter standing crop	5.333	0.05	11.3
A. rosea	1. soil depth 2. soil density	7.307	0.01	32.5
A. muldali	1. litter standing crop	14.976	0.001	26.3
O. cyaneum	1. drying out (Jly.—Aug)	4.953	0.05	10.6
Intermediate:				
A. chlorotica	none	—	—	—

(epigées) although affected in their distribution by litter standing crop are more significantly associated with soil depth and the moisture regime of the soil. In the case of *D. rubida* it should be noted that a significant correlation with the drying out properties of the soil only occurs at the 5% level of probability. Amongst the deep burrowing (anécique) species the distribution of *L. terrestris* is clearly associated with soil depth whereas that of *A. longa* is only just significantly correlated ($p = 0.05$) with the drying out properties of the soil in July—August. The distributions of the horizontal burrowers (endogées) are variously affected by different site characteristics, the most statistically significant associations being *A. muldali* with the litter standing crop and *A. rosea* with soil depth. *A. caliginosa* is only just significantly associated ($p = 0.05$) with litter standing crop and a similar level of significance can be seen with *O. cyaneum* and soil drying out properties in July—August. With *A. chlorotica*, the intermediate form, no statistically significant relationships with site characteristics were established.

One site factor it was not possible to study in relation to earthworm distribution by means of regression analysis was the ground flora; this was because quantitative measures of the density of the individual plant species were not available. However data from each individual grid square on the co-occurrence of each of the earthworm species with each of the thirty nine species of the ground flora (table 1) were available and an analysis was made by means of 2×2 contingency tables. Table 5 summarises those results where an earthworm species was shown to be significantly associated with particular plant species. It is of interest to note that the two species of earthworm showing highly significant associations with plant species were only shown to have correlations of low significance ($p = 0.05$) with the site characteristics used in the multiple regression analysis.

Table 5. The significant associations between earthworm species and ground flora plant species as shown by 2×2 contingency table analysis

Earthworm species	Plant species	χ^2	P
A. longa	*M. perennis*	7.15	0.001
A. caliginosa	*Q. robur* (seedlings)	10.49	0.001
	G. luteum	10.49	0.001
	D. glomerata	10.49	0.001
	A. stolonifera	10.49	0.001
	S. media	4.87	0.01
	G. verum	4.87	0.01
	S. vulgaris	4.87	0.01
	L. perenne	4.87	0.01

8. Discussion

The numbers of earthworm species reported from woodland habitats varies between two for beech woods (Balzer 1956; Drift 1951) and coniferous plantations (Reynoldson 1966; Satchell 1967) and fourteen for willow — *Salix* spp. (Piearce 1972a). Within this range beech woods usually support 6—8 species (see Nordström and Rundgren 1973); clearly, the ten species found to occur in the present study indicate that Brogden's Belt (an overmature beech wood on Corallian limestone) can be termed species rich as far as earthworms are concerned.

The number of species present in a particular habitat is a simple measure of diversity but as such it fails to take account of species abundance patterns or sample size (Krebs 1972; Ricklefs 1973). A simple index such as species number is therefore not wholly suitable for comparing faunal diversity in similar habitat types of different size. Indices which are suitable for purposes of comparison have been devised, they are independent of sample size and take into account the relationships of numbers of species to numbers of individuals (for excellent summaries see Southwood 1966; Krebs 1972). In the present study the earthworm diversity of Brogden's Belt was compared with earthworm diversity in the two Swedish beech woods studied by Nordström and Rundgren (1973). Two indices of diversity were used, Simpson's index which is based on probability theory and the Shannon-Wiener function derived from information theory. It should be noted that species diversity measured by the Shannon-Wiener function increases with a greater number of species and with a more even or equitable distribution of abundance amongst the species (Krebs 1972). Bearing this in mind it is clear from table 3 that the two diversity indices used gave rise to similar results, the Swedish Beech wood 17 with only eight species had the highest species diversity while Brogden's Belt and Beech wood 4, with ten and six species respectively, produced very similar species diversity values. More informative are the two equitability indices, both of which are derived from the Shannon-Wiener function. The Lloyd and Ghelardi (1964) index is considered to be the more ecologically realistic as it appears to represent the maximum ecological diversity attainable and as such reflects the ecological fullness of the habitat. Table 3 shows clearly that with six and eight species respectively the two Swedish beech woods have probably attained maximum ecological diversity with respect to earthworms; in contrast Brogden's Belt with ten earthworm species is not yet as ecologically diverse as it theoretically could be. It must be concluded that Brodgen's Belt has a greater habitat heterogeneity than either of the two Swedish beech woods.

Of the ten species recorded from Brodgen's Belt three *(A. chlorotica, A. muldali* and *D. mammalis)* have not, to our knowledge, been recorded from beech woods by anyone other than Bouché (1972) in France; in all cases the beech was growing in soils overlying a calcareous substrate.

The extensive records of Bouché (1972) show that eight of the ten species collected in the present study occur in a wide variety of habitats, for example coniferous forests, deciduous woods and pastures. The two exceptions are *A. muldali* and *D. mammalis* which do not appear to have been recorded from coniferous woodlands. With such an ubiquitous distribution of the species comprising the earthworm fauna of Brogden's Belt it is difficult to establish whether the species spectrum can be considered characteristic of beech woodlands, nevertheless an attempt has been made. Using the dominance data summarised by Nordström and Rundgren (1973) it was possible to compare the earthworm faunas of 36 beech woods, 37 deciduous woods other than beech, 38 coniferous woods and 43 permanent pastures. For each earthworm species in each of the four major habitat types the ratio

$$\frac{\text{number of occasions the species was dominant}}{\text{total number of occasions the species occurred}}$$

can be used as an index of the relative importance of a species between habitats, Table 6 shows the ratios calculated for each species in each major habitat; clearly, of the ten species recorded in the present study *A. caliginosa*, *A. rosea*, *D. rubida* and *L. castaneus* can be considered predominantly beech wood forms in that they have the highest index in this habitat. *Lumbricus terrestris* appears to be a deciduous woodland/pasture form while *A. longa*, *A. chlorotica* and *O. cyaneum* are most characteristic of permanent pastures. *Dendrobaena mammalis*, and *A. muldali* never dominated any of the earthworm faunas studied. Brogden's Belt, with *A. caliginosa*, *A. rosea* and *L. castaneus* together comprising 68–76 % of the total number of earthworms, may thus be considered fairly typical of many beech woods. On the other hand it is atypical in that *L. rubellus*, *D. octaedra*, and *O. lacteum*, all of which are quite common in other beech woods did not occur in our study area; moreover *A. muldali*, which was abundant in Brogden's Belt, has not been reported from many other beech woods.

The characteristic/uncharacteristic paradox of the Brogden's Belt species spectrum in relation to other beech woods is of interest from the species association viewpoint. Nordström and Rundgren (1973) from their own studies of beech found the typical species association to be *Dendrobaena octaedra — Lumbricus rubellus*, of which neither species was found in the present study. Using a variety of association analyses (Sørensen 1948: Cole 1949 and Fager 1957) two associations were distinguished in Brogden's Belt **(A)** *A. rosea*, *L. terrestris*, *L. castaneus* and *D. mammalis* and **(B)** *A. rosea*, *A. caliginosa*, *L. terrestris* and

Table 6. Indices of the relative importance of species between major habitats

Species	Major habitat type			
	Beech wood (n = 36)	Deciduous wood (n = 37)	Coniferous wood (n = 38)	Permanent pasture (n = 43)
* *A. caliginosa*	**0.55**	0.29	0.00	0.25
* *A. chlorotica*	—	0.00	—	**0.08**
A. limicola	0.00	0.25	—	**0.29**
* *A. longa*	0.00	0.00	—	**0.05**
A. nocturna	—	—	—	**0.33**
* *A. rosea*	**0.13**	0.11	—	0.05
* *A. muldali*	—	—	—	—
B. eiseni	—	0.00	—	0.00
* *D. mammalis*	—	—	—	0.00
D. octaedra	0.60	0.03	**1.00**	0.00
* *D. rubida*	**0.08**	0.00	0.00	0.00
E. tetraeda	0.00	0.00	—	0.00
* *L. castaneus*	**0.09**	0.00	0.00	0.00
L. festicus	—	0.00	—	0.00
L. rubellus	**0.29**	0.04	0.15	0.09
* *L. terrestris*	0.00	**0.04**	0.00	**0.04**
* *O. cyaneum*	0.00	0.00	—	**0.03**
O. lacteum	**0.29**	0.00	—	0.02

* signifies that the species was found in Brodgen's Belt.

$$\left(\text{Index} = \frac{\text{no. of occasions species was dominant in habitat}}{\text{no. of occasions species occurred in habitat}}\right)$$

possibly *D. mammalis*. On criteria outlined by FAGER (1957) association **A** was chosen as the more important association but it should be noted that association **B** is very similar to the *A. rosea*, *A. caliginosa*, *L. terrestris* association described by NORDSTRÖM and RUNDGREN (1973) as typical of deciduous woods of the "meadow" type, permanent pastures and Juniperus pasture. Beech is known to grow on a wide variety of soil types (TANSLEY 1939) and this is reflected by the three beechwoods compared in this study. Brogden's Belt grows on Corallian limestone (soil pH 7.3—8.0). Beech wood 4 was on glacifluvial sand (soil pH 3.5—4.2) and Beech wood 17 on Baltic moraine with a clay content of 15—25% and a soil pH of 5.5—6.6 (NORDSTRÖM and RUNDGREN 1974). Clearly, soil rype rather than dominant tree cover governs the species associations found in the three beech woods. SATCHELL (1955) has argued that pH is an important factor governing earthworm distribution; BOUCHÉ (1972) PIEARCE (1972a) and NORDSTRÖM and RUNDGREN (1973) have provided additional evidence to support this contention; they have also variously indicated that the quantity and quality (C/N ratios) of organic material as well as the moisture and calcium carbonate ($CaCO_3$) content of the soil are important. The different earthworm associations found in the Swedish and English beechwoods can be explained by the fact that *D. octaedra* and *L. rubellus* are acidophile, euryhumic, and inhabit soils with a minimum C/N ratio >8 and mean $CaCO_3$ content of $<4\%$; whereas *A. rosea*, *A. caliginosa*, *L. terrestris*, *L. castaneus* and *D. mammalis* are all either basiphil or neutrophil, stenohumic, and inhabit soils with a minimum C/N ratio <8 and a mean $CaCO_3$ content $>4\%$.

The presence of a particular species association in a number of habitats indicates uniformity of species composition and implies that the general habitat conditions necessary for existence are shared by all the species; however, within a single habitat the identification of a species association does not give any idea of the similarities in the specific requirements of the individual species. Ordination is a process by which species can be ordered along a gradient and hence it provides additional information about the similarities in requirements of the different species. In the present study the ordination procedure suggested by MOUNTFORD (1962) was adopted and it is clear from Figure 6 that high indices of similarity distinguish three pairs of species from within the two associations identified, *A. rosea — A. caliginosa, L. castaneus — D. mammalis*, and *L. terrestris — (D. rubida)*. The separation agrees well with the classification proposed by BOUCHÉ (1972) in that *A. rosea* and *A. caliginosa* are both inhabitants of the mineral-organic stratum and are strictly "endogées"; the other mineral-organic horizon dwellers found in Brogden's Belt show slight differences, *A. muldali* is described as "hypoendogé" and *O. cyaneum* as "épiendogé". *Lumbricus castaneus* and *D. mammalis* are both litter dwellers (épigées) according to BOUCHÉ (1972) and hence this species pair also accords with his classification. The pairing of *L. terrestris* and *D. rubida* appears anomalous in that *L. terrestris* is a deep burrower (anécique) whereas *D. rubida* is a litter dweller (épigé). The apparent paradox is resolved when it is realised that *D. rubida* aggregates in the decomposing leaf bundles at the entrance to burrows of *L. terrestris* (BOLTON 1969).

The distributions according to abundance of the ten species found in Brogden's Belt were explored by means of computer derived maps (fig. 8, 10 and 13—19). The factors governing species distribution on the study site were also examined but by means of linear multiple regression (table 4) and 2×2 contingency tables (table 5).

Distributions in terms of abundance were shown not to be uniform over the study site for either the total earthworm fauna or the individual species. This was to be expected and lends support to the statement made earlier in the discussion about maximum ecological diversity and habitat heterogeneity.

Amongst the litter dwellers the distribution according to abundance of *D. mammalis* (fig. 8 and 9) showed good agreement with litter standing crop during the winter (fig. 2b) but appeared to be susceptible to the drying out of the litter in summer. These observations were confirmed by statistical analysis when it was demonstrated that soil depth, the drying out properties of the soil in June—July, and litter standing crop were significantly correlated with the distribution patterns (table 4). The results are in accord with the general conclusions of BOUCHÉ (1972) for this species, while the movement of *D. mammalis* into the soil during the summer is no doubt related to the observation of SAUSSEY (1956) that this form is frequently associated with the burrows of mineral-organic horizon dwellers.

Another litter dweller, *L. castaneus*, had a similar distribution pattern (fig. 10) to that of *D. mammalis* and the relationship between distribution according to abundance and litter standing crop (fig. 2) was clear in all seasons. The detection of any movement into the soil by *L. castaneus* during the spring and early summer (fig. 11) was possibly obscured by recruitment to the litter population between March and July; although, as table 4 shows, the distribution according to abundance of the litter dwelling *L. castaneus* was positively correlated with both litter standing crop and soil moisture characteristics. The soil dwelling members of this species showed a significant correlation with soil depth and soil density. NORDSTRÖM and RUNDGREN (1974) provided similar evidence to that given above and showed that although *L. castaneus* concentrated in the superficial organic horizons it was also dependent on the textural composition of the lower horizons. BOUCHÉ (1972) describes this species as moisture loving and "épigé straminicole".

The third litter dwelling species, *D. rubida*, was not widespread over the site but its association with the decomposing leaf bundles of *L. terrestris* (BOLTON 1969) and the possible drying out properties of the soil (table 4) might well account for its restricted distribution in Brogden's Belt. NORDSTRÖM and RUNDGREN (1974) consider *D. rubida* to be acidophilic (although SATCHELL (1955) classified it as ubiquitous) and this may also account in part for its limited distribution and abundance in the base-rich soils of the study site. BOUCHÉ (1972) indicates that *D. rubida* is relatively acid tolerant and prefers habitats of high carbon content (mean carbon content >75%) and high moisture content.

Of the deep burrowing (anécique) earthworms present on the study site *L. terrestris* was the most numerous (table 2) and widespread (fig. 13). The distribution according to abundance of this species showed the expected significant correlation with soil depth (fig. 1b and table 4). Although *L. terrestris* is an effective litter feeder (LINDQUIST 1941) is has been pointed out by SATCHELL (1967) that besides litter it ingests a considerable amount of soil; it is not surprising therefore that NORDSTRÖM and RUNDGREN (1974) found a significant positive relationship between the amount of organic matter in the soil between 20 and 60 cm and abundance.

Allolobophora longa, the remaining deep burrowing form in Brogden's Belt, was not very abundant (table 2). Its distribution pattern (fig. 14) when compared with those of the site characteristics (fig. 1—3) indicated that soil depth (fig. 1b) and ground flora cover (fig. 1d) might be of importance to this species. Multiple regression techniques showed only the drying out properties of the soil in July—August to be significant (table 4) and even then at a low level (P = 0.05). Analysis by 2×2 contingency tables showed a highly significant relationship between the distribution pattern of *A. longa* and that of *Mercurialis perennis* (table 5). NORDSTRÖM and RUNDGREN (1974) demonstrated a significant relationship with the organic matter content of the soil between 20 and 60 cm depth and the abundance of *A. longa*. Drought is known to reduce surface casting (EVANS and GUILD 1947) and to induce summer diapause in *A. longa* (SATCHELL 1967). Amongst other species *A. longa* shows an ability to distinguish between different kinds of litter as food (LINDQUIST 1941). *Mercurialis perennis* is a preferred food of deep burrowing forms (SATCHELL 1967) and there is little reason to doubt that soil moisture characteristics and food type govern the distribution of *A. longa* in Brogden's Belt.

In terms of number of species and abundance, the earthworms living in the mineral-organic horizons were the most numerous on the study site. ***Allolobophora caliginosa*** was the dominant earthworm species (table 2) and occurred in relatively high densities over most of Brogden's Belt. Comparison of its distribution pattern (fig. 15) with those for various site characteristics (fig. 1—3) gave no clear indication of the factors governing distribution or abundance. Multiple regression analysis indicated a significant correlation between abundance and litter standing crop but only at the 5% probability level (table 4). The relationship with litter standing crops is probably not a causal one in that litter has been shown to accumulate where ground vegetation occurs (compare fig. 1b and 2d). A highly significant relationship was demonstrated by contingency table analysis when the presence of *A. caliginosa* was shown to be correlated with the occurrence of eight species from the ground flora (table 5). WATERS (1955) has indicated that dead roots are important to *A. caliginosa* and, given that microorganisms accumulate in their vicinity, this is compatible with the views of BARLEY (1959) and GRAFF (1964) that this species feeds on microorganisms. Only two of the eight plant species with which *A. caliginosa* showed significant associations are annuals (*Stellaria media* (L.) VILLARS and *Senecio vulgaris* L.) but it is clear that the quantity of dead root material shed by the eight species will be quite high; it is thus possible to account for the distribution of *A. caliginosa* within Brogden's Belt. PIEARCE (1972b) has shown that this species contains a lot of well decomposed organic matter in its gut.

Allolobophora rosea ranked second in abundance on the study site (table 2), it was widely distributed (fig. 16) and appeared to be correlated with soil depth (fig. 1b). Multiple regression analysis confirmed this and also indicated that soil density was important. BOLTON (1969) showed that *A. rosea* comminutes particles of plant debris from the soil and actively selects for ingestion the more organic fraction of the soil, this is in accord with NORDSTRÖM and RUNDGREN's (1974) results which showed a significant relationship between *A. rosea* abundance and the organic content of the soil between 20 and 60 cm depht. Data to test this relationship were not obtained during the present study.

The third of the mineral-organic soil species, *A. muldali*, was common on the study sites (Table 2) but has not been recorded from many other sites. BOUCHÉ (1972) has reported this species from a variety of habitats in France and it would appear to be most common in argillo-calcareous soils. Within Brogden's Belt it occurred over much of the site (fig. 17) and comparison of its distribution pattern with those of the site characteristics (fig. 1—3) showed the closest relationship with litter standing crop (fig. 2). This relationship was confirmed by multiple regression analysis (table 4) and is compatible with BOUCHÉ's (1972) classification of *A. muldali* as "hypoendogé".

Octolasion cyaneum is the last of the true mineral-organic soil dwellers which occurred in Brogden's Belt. It was relatively common (table 2) and was found over much of the site (fig. 18). Comparison of its distribution pattern with those of site characteristics (fig. 1—3) failed to reveal any obvious relationships. Multiple regression analysis demonstrated a significant correlation (P = 0.05) with soil drying out properties in July—August (table 4). Bouché (1972) classified *O. cyaneum* as "épiendogé" and described it as being typical of humid soils. Gerard (1964) pointed out that this species is abundant in argillo-calcareous and moist soil. From studies of the gut contents and faeces of *O. cyaneum* Bolton (1969) concluded that it feeds by passing large quantities of the substrate through its intestinal tract where virtually all the soil organic matter is assimilated.

The distribution pattern of the intermediate form, *A. chlorotica* is shown in fig. 19. It was not numerous on the study site (table 2) and its distribution was restricted. All types of analysis failted to provide any information about the factors governing the distribution of this species. Gerard (1964) stated that *A. chlorotica* is often numerically dominant in pastures, arable land and gardens (see table 6) where it is usually found among or near the roots of plants. No evidence of the root habitat preference was obtained in this study although Piearce (1972b) states that *A. chlorotica* ingests material of a similar nature to that taken by *A. caliginosa*.

Satchell (1967) pointed out that physico-chemical characteristics of the soil, vegetation type and land management all affect earthworm distribution; the comparison of different habitats outlined in the present paper support this viewpoint. However, Satchell (1967) also contended that most of what is known of earthworm behaviour and distribution can be interpreted in terms of the two basic requirements, water and food; clearly this argument is most relevant when species distribution within a single site is being considered. In this study the moisture characteristics of the soil were important in governing the distribution in time and space of the two major litter dwellers, *D. mammalis* and *L. castaneus*. Together with *p*H they probably also played a part in determining the low numbers and restricted distribution of *D. rubida*. However, while the well documented relationship between *O. cyaneum* distribution and moist calcareous soils was again demonstrated, *A. longa* showed a more significant correlation with the food plant *Mercurialis perennis* than with soil moisture.

Satchell (1963, 1967) produced experimental evidence which showed that earthworm populations increase when additional organic matter is provided and, on the basis of studies with *L.terrestris*, suggested that there is probably intense competition for food amongst the soil fauna. Intra-specific competition for food probably is intense but in the context of inter-specific competition for food the present study suggests a considerable degree of ecological separation between the earthworm species. Amongst the litter dwellers *D. mammalis* and *L. castaneus* are separated by temporal and spatial differences in distribution (fig. 9 and 11); moreover *D. mammalis* is "pholeophil" and associated with the burrows of inhabitants of the mineral-organic horizons (Saussey 1956) while *L. castaneus* is "straminicole" and associated with leaf litter proper (Bouché 1972). *Dendrobaena rubida* appears to be separated from the above two species by its association with the decomposing leaf bundles of the deep burrowing *L. terrestris* (Bolton 1969). In Brogden's Belt the deep burrowing *A. longa* is strongly associated with a potential food plant *(M. perennis)* whilst *L. terrestris* feeds on litter and organic matter in the soil (Satchell 1967). Of the four species inhabiting the mineral-organic layer *A. muldali* is "hypoendogé" (Bouché 1972) and lives in the compact soil below the *A* horizon whereas *O. cyaneum* is "épiendogé" (Bouché 1972), inhabits the *A* horizon and unpreferentially assimilates all types of organic matter in the soil (Bolton 1969). *Allolobophora caliginosa* and *A. rosea* are strictly "endogées" (Bouché 1972) but the former feeds on microorganisms in the vicinity of dead roots (Waters 1955; Barley 1959 and Graff 1964) while the latter actively selects its food from the plant debris of the soil (Bolton 1969). There can be little doubt that ecological separation with respect to distribution and food does occur between the earthworm species of Brogden's Belt and this must have a major effect in reducing interspecific competition.

9. Summary

Ten species of earthworm were recorded from a *Fagus sylvatica* L. woodland in southern England Compared with the lumbricid fauna of two Swedish beech woods (6 & 8 species respectively) the "equitability" component of species diversity was low, which implies that maximum ecological diversity has not yet been attained in the 150 year old English woodland.

Two species associations were identified (i) A. rosea — L. terrestris — L. castaneus — D. mammalis and (ii) A. rosea — A. caliginosa — L. terrestris — D. mammalis. *Allolobophora caliginosa* was the numerically dominant form and together with *A. rosea* comprised approximately 65 % of the total numbers of earthworms.

The species associations recorded from the study site differed from the Dendrobaena octaedra — L. rubellus association described from beech woods in Sweden. The differences are explained in terms of soil characteristics, *p*H was important in this respect (present study site *p*H 7.3—8.0, Swedish sites *p*H 3.5—4.2 and 5.5—6.6 respectively).

Computer derived maps of distribution according to abundance are given for the within site distributions of each of the ten species. Multiple regression and 2 × 2 contingency table analyses showed that soil depth, soil moisture characteristics, litter standing crop and ground vegetation type are all important factors which govern the local distributions of individual species.

It is suggested that inter-specific competition between earthworms on the study site (particularly for food) is reduced by ecological separation of the species in time and space and by different food preferences.

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